feeding by parasites in heavy infections can lead to complete destruction of the gonads and sterilization of the host (parasitic castration).

From a comparison of normal and infected digestive gland histology, the presence of rediae appears to reduce the number of gland acini. This reduction is probably due to active ingestion by redial stages, as reported by PORTER et al. (1967), READER (1971) and ROBSON & WIL-LIAMS (1971), though little direct histologic evidence for this pattern of redial feeding behavior is noted in Cerithidea californica. Perhaps mechanical pressures of developing parasites (JAMES, 1965; PORTER, 1970; READER, 1971) or the presence of secretions or excretions of parasite origin (CHENG & BURTON, 1965; PORTER, 1970; CHENG et al., 1973) also contribute to the decrease in acinar number. This is supported by the observation that heavy infections of Spelotrema nicolli and the strigeid, both utilizing sporocysts which do not feed by pharyngeal ingestion, also result in a reduction of digestive tubules. YOSHINO (1974) has reported some light and electron microscopic evidence for cellular degeneration in deeper digestive gland tissues of C. californica infected with rediae of Euhaplorchis californiensis. This suggests that damage to the digestive gland acini may be through indirect as well as direct redial/tissue contact.

The occurrence of multiple trematode infections within a single host is well documented, especially for marine prosobranchs. Multiple infections have been reported by HUNTER (1942) and MARTIN (1955) in *Cerithidea californica;* VERNBERG *et al.* (1969) in the mudsnail, *Nassarius obsoletus;* and ROBSON & WILLIAMS (1970) in the periwinkle, *Littorina littorea* (Linnaeus, 1758). Both MARTIN (*op. cit.*) and VERNBERG *et al.* (*op. cit.*) mention a nonconformity between the number of observed multiple infections, especially those involving echinostome species, and the number of infections expected by random combination. A similar situation also has been noted for multiple infections in freshwater gastropods (CORT et al., 1937; BOURNS, 1963; LIE, 1966). Multiple infections in C. californica from Goleta Slough do conform generally to expected frequencies, even when involving some species of echinostomes. The strigeid represents a notable exception, being observed only in double infections, never singly. This suggests that establishment of strigeid infections in Cerithidea may depend upon a prior infection of another trematode species which has in some manner altered the host's susceptibility to infection. A synergistic relationship such as this, however, can only be confirmed by controlled experimental infections in the laboratory.

In a recent review of mechanisms governing interspecific larval trematode interactions within a host, DE-COURSEY & VERNBERG (1974) summarize the major kinds of interaction recognized in the literature today. They include: 1) complete coexistence, 2) preferential tissue selection, 3) longitudinal or radial displacement of one species, 4) cannibalism of one species on another (direct antagonism), 5) indirect antagonism, 6) hyperparasitism, and 7) alteration of the host's internal environment affecting its resistance. The occurrence of Renicola buchanani (mantle wall) with Euhaplorchis californiensis or the strigeid (visceral spiral) is possible since the selection of different tissue types allows for spacial separation between the species. However, when E. californiensis and the strigeid (both found primarily in the gonadal tissues) are present concurrently, E. californiensis (dominant species) will displace the strigeid, forcing it into the digestive gland, a locus of secondary preference (Figure 10). One combination involving E. californiensis and the echinostome, Parorchis acanthus, was not observed during the present survey, though, according to random chance, this combination should have occurred about 3 times. However, during a recent study by the author of Cerithidea's cellular blood system, one such combination was encountered. Histologic examination reveals Par-

Explanation of Figures 8 to 11

Figure 8a:Cross-section of intestine (rectal region) in the mantle wall of an uninfected *Cerithidea californica*. Hematoxylin and eosin. $approximately \times 100$

Figures 8b, 8c: Sporocysts of *Renicola buchanani* (toluidine blue) and rediae of *Catatropis johnstoni* (hematoxylin and eosin), respectively, infecting the mantle region of *Cerithidea*. × 120

Figure 9: Infection of gonadal region by sporocysts of the strigeid (furcocercous cercaria). Toluidine blue. × 120 Figure 10: Double infection of the gonadal and digestive gland

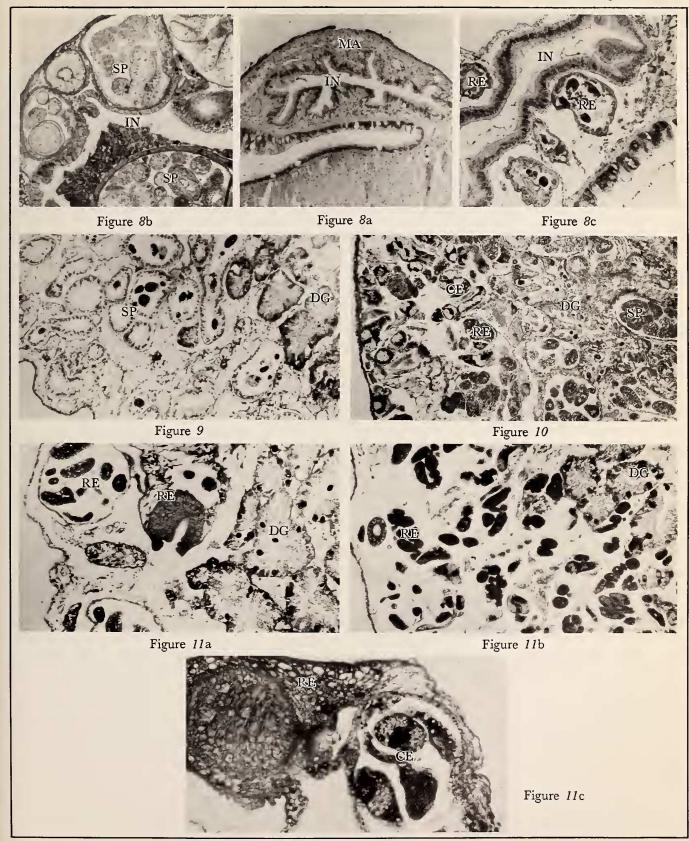
> DG – Digestive Gland Tubules CE – Cercarial Stage(s) IN – Intestine

regions by larval stages of *Euhaplorchis californiensis* and strigeid sporocysts. Toluidine blue. × 120

Figures 11a, 11b, 11c: Double infection of the gonadal region by Parorchis acanthus rediae, and rediae and cercariae of Euhaplorchis californiensis. Toluidine blue. a) P. acanthus rediae occupying gonadal area of the anterior visceral spiral \times 120. b) E. californiensis rediae and cercariae in the posterior region of the visceral spiral. \times 120. c) Parorchis rediae with ingested cercariae of Euhaplorchis. \times 300

MA – Mantle Tissues RE – Redial Stage(s) SP - Sporocyst Stage(s) THE VELIGER, Vol. 18, No. 2

[YOSHINO] Figures 8 to 11





orchis to be strongly antagonistic towards E. californiensis, laterally displacing, by active predation, the heterophyid in a posterior direction in the host (Figures 11a, 11b, 11c). These observations lend support to the negative inference that double infections involving Parorchis rediae are rare due to their antagonistic behavior towards other trematode species. A single observation is not, however, very reliable and confirmation of this kind of interaction must await double infection experiments on Ceri-

ACKNOWLEDGMENTS

thidea, similar to those being performed on freshwater

planorbids (reviewed by LIM & HEYNEMAN, 1972).

I wish to express my appreciation to Dr. Elmer R. Noble (University of California, Santa Barbara) for his encouragement and support during this study, and for his guidance in the preparation of the manuscript. I would also like to thank Mike Moser and Gary Alderson for their critical review of the final manuscript. This study was supported in part by NSF Grant GA 34144 to Dr. E. R. Noble.

Literature Cited

ADAMS, JOEL E. & WALTER E. MARTIN

- 1963. Life cycle of *Himasthla rhigedana* Dietz, 1909 (Trematoda: nostomatidae). Trans. Amer. Microsc. Soc. 82: 1-6 Echinostomatidae). BOURNS, T. K. R.
- 1963. Larval trematodes parasitizing Lymnaea stagnalis appressa Say in Ontaria with emphasis on multiple infections. Canad. Journ. Zool. 41: 937 - 941

CHENG, THOMAS CLEMANT & RICHARD W. BURTON

- Relationships between Bucephalus sp. and Crassostrea virginica: 1965. Histopathology and sites of infection. Chesapeake Sci. 6: 3 - 16
- CHENG, THOMAS CLEMANT, JOHN T. SULLIVAN & KEVIN R. HARRIS 1973. Parasitic castration of the marine prosobranch gastropod Nassa-rius obsoletus by sporocysts of Zoogonus rubellus (Trematoda): Histo-Journ. Invert. Pathol. 21: 183 - 190 pathology.

CORT, WILLIAM W., DONALD B. MCMULLEN & STERLING BRACKETT

1937. Ecological studies on the cercariae in Stagnicola emarginata (Sowerby) in the Douglas Lake region. Journ. Parasit. 23: 504 - 532 DECOURSEY, PATRICIA J. & WINONA B. VERNBERG 1974. Double infections of larval trematodes: competitive interactions.

- In: Symbiosis in the Sea (W. B. Vernberg, ed.); xvi+276 pp.; illust. Univ. So. Carolina Press, Columbia, S. C.
- HUNTER, WANDA S.
- 1942. Studies on cercariae of the common mud-flat snail, Cerithidea californica. Ph. D. thesis, Univ. Calif. Los Angeles; 129 pp.; 51 text figs.; 5 charts; 12 tables

JAMES, BRIAN LLOYD

The effects of parasitism by larval Digenea on the digestive gland 1965. of the intertidal prosobranch, Littorina saxatilis (Olivi) subsp. tenebrosa Parasitology 55: 93 - 115 (Montagu).

JUREE, RONALD M. & HOWARD R. LEACH

California shore bird survey, 1969-1970. Spec. Wildl. Reprt. 1971. Calif. Dept. Fish & Game: 91 pp.; illust.

- LIE, KIAN J. 1966. Antagonistic interaction between Schistosoma mansoni sporocysts
 - and echinostome rediae in the snail Australorbis glabratus. (London) 211: 1213 - 1215

LIM, HOK-KAN & DONALD HEYNEMAN

Intramolluscan inter-trematode antagonism: a review of fac-1972 tors influencing the host-parasite system and its possible role in bio-logical control. In: Advances in Parasitology (B. Dawes, ed.); vol. 10; 412 pp.; illust. Academic Press, London & New York MARTIN, WALTER E.

- 1950a. Euhaplorchis californiensis n. g., n. sp., Heterophyidae, Trema-toda, with notes on its life-cycle. Trans. Amer. Microscop. Soc. 69: 194 - 209
- 1950b. Parastictodora hancocki n. gen., n. sp. (Trematoda: Heterophy-idae), with observations on its life cycle. Journ. Parasit. 36: 360 370
- 50c. Phocitremoides ovale n. gen., n. sp. (Trematoda: Opisthorchi-dae), with observations on its life cycle. Journ. Parasit. 36: 1950c
- 552 558 1951. Pygidiopsoides spindalis n. gen., n. sp. (Heterophyidae; Trematoda), and its second intermediate host. Journ. Parasit. 37: 297 - 300
- 1955. Seasonal infections of the snail, Cerithidea californica Halde-man, with larval trematodes. In: Essays in the Natural Sciences; Alan Hancock Foundaton; 335 pp.; illust.; Univ. So. Calif. Press, Los Angeles

1956. The life cycle of Catatropis johnstoni n. sp. (Trematoda: Notocotylidae). Trans. Amer. Microsc. Soc. 75: 117 - 128 MARTIN, WALTER E. & V. L. GREGORY

1961. Life cycle of Acanthoparyphium spinulosum Johnston, 1917 (Echinostomatidae: Trematoda). Journ. Parasit. 47: 777-782 MARTIN, WALTER B. & V.L. GREGORY

1951. Cercaria buchanani n. sp., an aggregating marine trematode. Trans. Amer. Microsc. Soc. 70: 359 - 362

MARTIN, WALTER E. & DAVID F. STEELE

Ascocotyle sexidigita sp. n. (Trematoda: Heterophyidae) with 1970. notes on its life cycle. Proc. Helminth. Soc. Wash. 37: 101 - 104

MAXON, MARION G. & WILLIS E. PEQUEGNAT Journ. Entomol. Zool. 1949. Cercariae from Upper Newport Bay. 4: 30 - 50

PORTER, CLARENCE A.

The effects of parasitism by the trematode Plagioporus virens on 1970. the digestive gland of its snail host, Flumenicola virens. Proc. Helminth. Soc. Wash. 37: 39-44

PORTER, CLARENCE A., IVAN PRATT & ALFRED OWCZARZAK

- Histopathological and histochemical effects of the trematode 1967. Nanophyetus salmincola (Chapin) on the hepatopancreas of its snail host, Oxytrema siliqua (Gould). Trans. Amer. Microsc. Soc. 86: 232 - 239
- Reader, TREVOR A. J.
 - The pathological effects of sporocysts, rediae and metacercariae 1971. on the digestive gland of Bithynia tentaculata (Mollusca: Gastropoda). Parasitology 63: 483 - 489

ROBSON, W. M. & I. C. WILLIAMS

- 1970. Relationships of some species of Digenea with the marine prosobranch Littorina littorea (L.). I. The occurrence of larval Digenea in L. littorea on the North Yorkshire coast. Journ. Helminth. 44: 153 - 168
- 1971. Relationships of some species of Digenea with the marine prosobranch Littorina littorea (L.). II. The effect of larval Digenea on the reproductive biology of L. littorea. Journ. Helminth. 45: 145 - 159
- VERNBERG, WINONA B., F. JOHN VERNBERG & FRED W. BECKERDITE, Jr. 1969. Larval trematodes: Double infections in the common mud-flat snail. Science 164: 1287 - 1288

Yoshino, Timothy P.

- Helminth parasitism in the Pacific killifish, Fundulus parvipinnis, 1972. from southern California. Journ. Parasitol. 58: 635 - 636 1974. Some fine structural observations on the histopathologic effects
- of larval Digenea on gastropod digestive gland acinar cells. Third Internat. Congress Parasitol. 3: 1704 - 1705 (abstract only)